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OBSERVATIONS ON POPULATIONS OF *TRIBOLIUM BREVICORNIS* LECONTE (COLEOPTERA: TENEBRIONIDAE). II. THE HABITAT NICHE OF A LOCAL POPULATION IN SOUTHERN CALIFORNIA

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Despite the great economic importance of flour beetles of the genus *Tribolium* MacLeay, little is known about their natural ecological niche. In the past, their role in nature was fabricated partly from naturalists' observations of the behavior of tenebrionids in general, and partly from their behavior under artificial conditions (in warehouses or in the laboratory). Thus, two main hypotheses about the role *Tribolium* plays in biological communities were proposed: 1. Because the beetles occur in the nests of bees, commonly inhabit stored products, and have been reported from under the bark of trees, some investigators (e.g., Magis, 1954) suggested that they are herbivores, feeding primarily on carbohydrates, fungi, or other materials of plant origin; and 2. Because many tenebrionids are scavengers or predaceous under natural conditions (e.g., species of Ulominae including several species of *Tribolium* invade nests of social insects), and because cannibalism was observed in laboratory cultures, some investigators (e.g., Linsley, 1944) suggested that they must be omnivores, surviving in nature as scavengers or semi-predators.

More recently, Park et al. (1965, 1970), and Sokoloff and Lerner (1967) from laboratory studies of single- and mixed-species populations of *Tribolium* in various media established that cannibalism is common and extensive. Sokoloff and Lerner have further emphasized that the interaction between *T. castaneum* (Herbst) and *T. confusum* du Val in laboratory cultures must be considered a predator-prey interaction rather than one of competition. (For a comprehensive review of the literature and an extensive discussion of this problem see Sokoloff, 1974.) From these recent laboratory observations, a third hypothesis can be advanced, namely, that in nature

Tribolium is a secondary or tertiary consumer, engaging in scavenging, predatory and cannibalistic activities.

Historically *Tribolium castaneum* and *T. confusum* are species long associated with stored products (Good, 1933). Their distribution and survival has been greatly influenced by man, through commerce and experimentation. Hence, these synanthropic species cannot be used effectively to test the three alternative hypotheses. However, other more primitive and less affected species of the genus may provide the information to fill this gap.

This paper will report field and laboratory observations of organisms associated with *Tribolium brevicornis* LeConte, a primitive species native to North America. Although recorded as a minor pest of stored products in other parts of California (Okumura and Strong, 1965; Strong, 1970), and as a serious pest to commercial growers of *Megachile pacifica* (Panzer) (Polk, 1979) in Idaho, this species appears to be little influenced by human activities in the area surveyed. Thus, the present information is relevant in establishing the habitat niche of *T. brevicornis,* and may contribute toward understanding other species whose habitat niche remains undefined.

Materials and Methods

Specimens for this investigation were collected from Waterman Canyon at an altitude of approximately 365 m (1200 ft.) located at the southwestern base of the San Bernardino Mountains, just outside the northern city limits of San Bernardino, California.

A survey of the flora was carried out using standard quadrat plot techniques.

To determine the diversity of organisms associated with *Tribolium brevicornis* in the decaying log biocoenosis we removed three 1 m sections from a downed alder (*Alnus rhombifolia* Nutt.) and one 1 m section from a dead sycamore (*Platanus racemosa* Nutt.) lying nearby which contained a hive of *Apis mellifera* Linnaeus. In the laboratory the pieces of alder were sectioned with a bandsaw either into longitudinal pieces 3 × 3 × 100 cm, or into cross-sections 3 cm thick. Organisms crawling on the surface were either preserved in alcohol, or (as in the case of *T. brevicornis*) saved and placed in standard flour beetle culture medium (19 parts wheat flour, 1 part brewer's yeast). To recover organisms from the galleries of carpenter bees the sections of the log were tapped against each other, and any loose material was allowed to fall on a sheet of white poster board. Sawdust produced from sectioning was sifted through a coarse silk-bolting cloth sieve to recover additional specimens.

The honeycomb from the beehive was removed from the log and frozen. Later the cells of the honeycomb were examined with a microscope for the presence of the various stages of the flour beetle.

Results and Conclusion

Habitat and flora.—The foothills adjacent to the *Tribolium brevicornis* collection site are typified by a mixture of Chamise Chaparral and Southern Oak Woodland plant communities (Munz and Keck, 1949) represented by *Adenostoma fasciculatum* H. & A., *Rhamnus californica* Esch., *Ceanothus* spp., *Yucca whipplei* Torr., *Prunus ilicifolia* (Nutt.) Walp., *Cercocarpus betuloides* Nutt. ex T. & G., *Heteromeles arbutifolia* M. Roem., *Rhus ovata* Wats., *R. laurina* Nutt. in T. & G., *Styrax officinalis* L., *Quercus dumosa* Nutt., *Q. crysolepis* Liebm., *Sambucus mexicana* Presl., and *Toxicodendron diversilobum* (T. & G.) Green. Naturalized escapes and native "weedy" Coastal Sage Scrub species were noted growing in areas disturbed by settlement.

The habitat of *Tribolium brevicornis* appears to be restricted to the more mesic streamside sites. *Alnus rhombifolia* is the dominant tree species at the streamside. Other tree species associated with this mesic area include *Acer macrophyllum* Pursh., *Umbellularia californica* (H. & A.) Nutt., *Platanus racemosa, Quercus crysolepis,* and *Salix* spp. Seventy-five *Alnus rhombifolia* trees were recorded from an area of about 480 m^2, ranging in basal area from 2246 cm^2 to 121 cm^2 and averaging about 734 cm^2.

Fauna.—The fauna found in the alder tree (Table 1) is typical of a decaying log. Many of the organisms (such as isopods, collembolans, termites, etc.) require mesic conditions for their survival. From Table 1 it is possible to speculate on fairly safe grounds that various arachnids (spiders and pseudoscorpions) and chilopods probably include the immature and adult stages of *Tribolium brevicornis* among their prey since their stereotyped predaceous and carnivorous habits are well known.

The reported feeding habits of Tenebrionidae, on the other hand, are variable, ranging from herbivory to omnivory to carnivory, and cannibalism (literature review in Sokoloff, 1974). Thus, it is not safe to speculate about the feeding habits of *Tribolium* on the basis of feeding habits of other genera within the family as Linsley (1944), Hinton (1948), Butler (1949) and Magis (1954) have done.

Surveys show that most of the wild species of *Tribolium* have been found mainly under bark, and occasionally synanthropic species return to and are captured in this same habitat. Hence, Good (1933, 1936), Linsley (1944), Butler (1949) and Magis (1954) have assumed that the primitive and natural habitat of *Tribolium* (and of the whole family) is under the bark or in decaying logs. On the other hand, reports also show that *Tribolium* in the various species groups have a tendency to become associated with other organisms, particularly Hymenoptera; e.g., *T. brevicornis* in nests of *Xylocopa* and *Anthidium, T. confusum* in nests of *Anthophora, Clisodon* and *Osmia* (Linsley and MacSwain, 1942), *T. destructor* Uyttenboogaart in nests of *Anthophora*

Table 1. Species associated with *Tribolium brevicornis* in decaying *Alnus rhombifolia* logs.

Phylum/ class	Order	Family	Genus or species if known
MOLLUSCA			
Gastropoda	Pulmonata	Limacidae	*Limax marginatus* Muller
ARTHROPODA			
Arachnida	Pseudoscorpionida		—
	Acari	Trombidiidae	—
		Ceraneidae	—
	Araneidae	Gnaphosidae	*Harpyllus* sp.
		Thomisidae	—[1]
		Theridiidae	*Pardosa* sp.[2]
Crustacea	Isopoda	Oniscidae	*Porcellio* sp.
		Armadillididae	*Armadillium vulgare* (Latreille)
Diplopoda			—
Chilopoda			*Scolopendra* sp.
Insecta	Collembola	Entomobryidae	—
	Isoptera	Kalotermitidae	*Incisitermes minor* (Hagen)
		Hodotermitidae	*Zootermopsis angusticollis* Hagen
	Hemiptera	Miridae	—
	Coleoptera	Carabidae	*Axinopalpus biplagiatus* (Dejean)
		Buprestidae	*Dicerca* sp. (prob. *horni* Crotch)
		Elateridae	—[3]
		Dermestidae	*Trogoderma orbatum* (Say)
		Bostrichidae	*Amphicerus cornutus* (Pallas)
		Ostomidae	*Tenebroides crassicornis* (Horn)
		Anthicidae	*Vacusus confinus* (LeConte)
		Rhizophagidae	*Rhizophagus* sp.
		Cucujidae	*Brontes dubius truncatus* (Motschulsky)
		Endomychidae	*Symbiotes montanus* (Casey)
		Tenebrionidae	*Blapstinus* sp.
			Metoponium convexicolle (LeConte)
			Tribolium brevicornis (LeConte)
		Cerambycidae	*Parandra marginicollis marginicollis* Schaeffer
		Curculionidae	*Rhyncolus* sp. *angulans* LeConte?
	Lepidoptera	Arctiidae	*Arachnis picta* Packard
	Diptera	Bombyliidae	*Anthrax tigrinus* (De Geer)
	Hymenoptera	Chrysididae	—
		Formicidae	*Camponotus* sp.
			Liometopum occidentale (Emery)
			Tapinoma sessile (Say)
		Sphecidae	*Ectemnius* sp.
		Megachilidae	—
		Apidae	*Xylocopa tabaniformes orpifex* (Smith)
CHORDATA			
Amphibia	Anura	Hylidae	*Hyla* sp.

[1] Immature. [2] Female with young in egg sac. [3] Early instar larva.

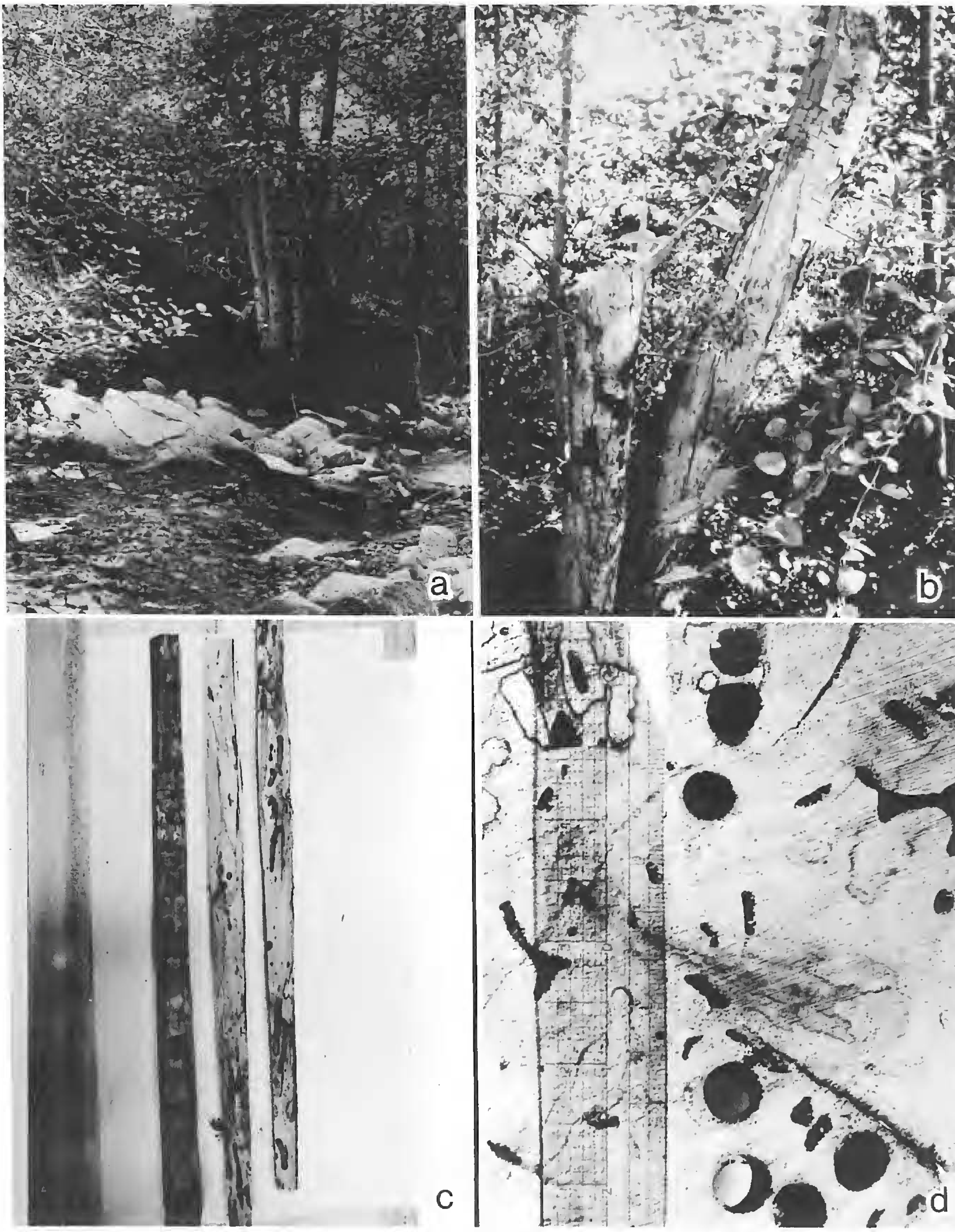

Fig. 1. a, Waterman Canyon creek with *Alnus rhombifolia*. b, Dead *A. rhombifolia* which served as nesting site for *Xylocopa*. c and d, Sections of *A. rhombifolia* showing galleries of *Xylocopa*.

and *Osmia* (Linsley, 1944), *T. anaphe* Hinton from cocoons of *Anaphe moloneyi* Druce (Hinton, 1948), *T. castaneum* from nests of *Megachile*, and *T. apiculum* Neboiss from nests of *Trigona carbonaria* Smith (Neboiss, 1962). *Tribolium madens* Charpentier was found in beehives in Silesia, and

Haragsim (1965) states that this species and *T. confusum* occur in beehives in Czechoslovakia. *Tribolium audax* Halstead has been obtained from cells of the bee *Megachile* (*Eutricharaea*) *rotundata* (Fabricius) (Leech, 1943; Halstead, 1969). *Tribolium myrmecophilum* Lea has been found in the nests of the ant *Iridomyrmex nitidus* Mayr (Lea, 1905) and has been recorded feeding on the pollen reserves of the Australian stingless bee *Trigona* (Rayment, 1932). *Tribolium antennatum* Hinton may occupy a similar habitat (Hinton, 1948). The literature fails to specify what kind of food the beetles have taken in. The present study shows that *T. brevicornis* occurs in decaying logs where the carpenter bee *Xylocopa tabaniformes orpifex* (Smith) has built galleries as nesting sites. *Tribolium brevicornis* was found in the galleries of *Xylocopa* and in other sites (but not in ant or termite nests). The species of tree apparently is of no importance. In the present case *T. brevicornis* was found in a decaying *Alnus rhombifolia,* but Linsley (1944) found it infesting a nest of *Xylocopa* in a decaying *Libocedrus decurrens* Torr.

Interestingly, *T. brevicornis* was found in *Xylocopa* nests but did not occur in a beehive of *Apis mellifera* found only three meters away, even though the latter would provide a richer source of food than the nests of *Xylocopa* (Sokoloff and Moore, unpublished). Over four dozen flour beetles were retrieved from the portion of the tree we examined. Unfortunately the vibration resulting from the sawing procedure caused the beetles to scatter, so that there were no aggregations in any one site of the log. The discovery of several large larvae of *T. brevicornis* verifies the fact that these beetles reproduce within the log. Some were found in galleries containing dead, dismembered *Xylocopa* adults. In a later study Sokoloff and Moore (unpublished) found *T. brevicornis* larvae feeding on pupae of *Xylocopa.* Further examination of *T. brevicornis* adults freshly captured in the field revealed the remains of carpenter bee exoskeletons in their digestive tracts.

Hence, the evidence gathered so far suggests that *T. brevicornis* is probably a secondary or tertiary consumer, engaging in scavenging, predatory, and possibly cannibalistic activities within the decaying log biocoenosis.

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